

SYMPOSIUM ON THE BIOLOGY AND EVOLUTION OF MOLLUSCA

A Symposium on molluscs was held in The Australian Museum from the 21st to the 25th May, 1979. It was organised by Dr. W.F. Ponder of The Australian Museum and Dr. A.J. Underwood of the University of Sydney with the assistance of the other members of The Australian Museum's Department of Malacology and TAMS volunteers, and students from the University of Sydney. Over 140 delegates attended the Symposium representing 10 countries and 47 papers and 26 posters were presented. The abstracts of the papers and posters are published in this issue of the Journal.

It was agreed by all that participated that the Symposium was an extremely worthwhile and successful event, not only in providing a forum for presenting information and for meeting people with similar interests but, particularly, in enabling scientists and students to gain a broader knowledge and appreciation of the Phylum containing the animals on which they have chosen to work.

Mollusca: the first hundred million years

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Molluscs appear to have evolved from free-living spiculose flatworms in the latest Precambrian (middle Vendian) between 650 and 600 million years ago. The oldest fossil molluscs are found in earliest Cambrian (early Tommotian) deposits of Siberia and China and are about 570 million years old. These diverse faunas show that 4 classes (Aplacophora, Monoplacophora, Gastropoda and Rostroconchia), 8 orders, and about 9 families of molluscs had appeared before the beginning of the Cambrian. The Precambrian molluscs were probably very small (~ 1 mm in size) and hence are inconspicuous as fossils.

Cambrian molluscs are not common fossils but important taxa have been described from the Early Cambrian of Siberia, China, western Europe and Massachusetts; the Middle Cambrian of Australia, Korea, Czechoslovakia and Canada; and the Late Cambrian of Antarctica, Australia, China and the United States. By contrast, Ordovician molluscs are common and widespread. These data suggest that: 1, at least 7 of the 8 classes of molluscs evolved prior to or during the Cambrian (570-500 million years ago); 2, the diversity of molluscs measured in terms of the numbers of orders and families present remained low (about 10 orders and 10 families) until the beginning of the Late Cambrian about 520 million years ago; and 3, an exponential increase in the diversity of molluscs commenced about 520 million years ago and lasted for about 40 million years until the end of the Early Ordovician. By the later Ordovician molluscan diversity had stabilised at 8 classes, 17 subclasses, about 30 orders and about 70 families.

Comparative studies of the skeletal anatomy (and inferred functional and soft-part morphology) of Cambrian and Ordovician molluscs suggest that the diversification of the phylum occurred in the following ways (dates in square brackets):

- 1, *Neopilina* - like limpet-shaped monoplacophorans (Scenellidae) evolved from chiton-shaped spiculose aplacophorans [Vendian].
- 2, animals with a taller curved shell, fewer pairs of gills, and fewer pedal muscle insertions (Helcionellidae) evolved from the Scenellidae [Vendian].
- 3, lateral narrowing of the helcionellid shell produced first the Stenothecidae [Vendian] and then ribeiriid rostroconchs [Vendian]. In these forms the shell-attached pedal muscles were enlarged anteriorly and posteriorly and reduced laterally.
- 4, the development of a flexible dorsal shell margin in primitive rostroconchs resulted in the evolution of the Bivalvia from the Rostroconchia [Early Cambrian]. The anterior and posterior pedal muscles of primitive rostroconchs were divided between left

and right valves in the Bivalvia. 6, asymmetric coiling of the descendants of some helcionellid monoplacophorans (Pelagiellidae, initiated torsion and the origin of the Gastropoda [Vendian]. Torsion occurred after one of the original pair of lateral shell-attached pedal muscles had been lost [Vendian]. 7, planispirally coiled bellerophon Monoplacophora evolved from helcionellid Monoplacophora [Middle Cambrian]. In tightly coiled forms the shell-inserted pedal muscles are reduced to a single pair. 8, elevation of the intake-tube of snorkel-bearing monoplacophorans (Yochelcionellidae) produced a tall, backward-curving shell [Middle Cambrian]. The first cephalopods may have evolved from septate descendants of the Yochelcionellidae by modifying the tissues of the snorkel to form a primitive siphuncle [Late Cambrian]. 9, enlargement of seven or eight dorsal spicules of a primitive aplacophoran produced the first chiton (*Matthevia*) [Late Cambrian]. Its series of dorsal spikes is homologous with the eight imbricate plates of younger polyplacophorans. 10, the better designed bivalves replaced more primitive rostroconchs [Middle Ordovician]. 11, cephalopods succeeded the Monoplacophora as the most diverse molluscan class [Ordovician].

Origin and relationships of the Mollusca

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Up to now, the question of molluscan origin has not been answered. As possible pathways of the lineage are discussed: the derivation of the molluscs from annelids or platyhelminthes as well as the combined evolution of molluscs and annelids from aschelminthes or larval stages of coelenterates. Also, the relationships between the classes of the Mollusca are not clear.

The classical arguments for the different interpretations are collated. Moreover, some new findings from paleontology, comparative anatomy, ultrahistology, and biochemistry are taken into consideration. Fossil species from the transition field between ancestors and molluscs are not known, and the possibility to find connecting links is minute. Therefore, the clearing up of the relations may be achieved only in recent species within the limits of circumstantial evidence. Particular stress is laid upon the valuation of the fine structure of specialized tissues and organs. Especially, the situation in flatworms, annelids and molluscs is considered. According to the method of Hennig, it is tried to evaluate the compiled characteristics as plesiomorphisms or apomorphisms and to collate them into a diagram of argumentation, following Hennig. This diagram reflects the probable interrelationships of the molluscan classes as well as the relationships to other phyla.

New Zealand Middle Cambrian Mollusca: their nature and bearing on early molluscan evolution

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Recent palaeontological research has shed new light on the identity of a number of the earliest molluscs that existed during the Cambrian Period, some 500 to 570 million years before present. This upsurge of interest in Cambrian molluscs has provided the impetus for a restudy of a variety of minute fossils that were known to occur in several New Zealand limestones of late Middle Cambrian age (about 520 million years before present).

The fossils occur as phosphatic moulds. By dissolving fragments of limestone in dilute acetic acid the fossils are readily recovered as part of the insoluble residue. Although internal moulds are most common, some fragments exhibiting external ornamentation are found occasionally. By comparison with modern day molluscs, Cambrian forms are of small size, and as none of the New Zealand forms have a maximum dimension of much more than two millimeters, they are of a size appropriate for examination by scanning electron microscope.

Despite the preservation of appreciable detail it is difficult to assign most forms to recognised higher taxonomic categories due to lack of diagnostic skeletal characters, such as muscle scars. The most commonly occurring fossil is the enigmatic *Pelagiella*, generally regarded as a mollusc and of world-wide distribution in Cambrian rocks. In addition to *Pelagiella*, genera known also from Australian Middle Cambrian strata include *Protowenella*, *Latouchella* and *Mellopegma*.

Of interest are two hitherto undescribed univalves, one showing strong lateral compression like *Mellopegma*, the other much less so, whose internal cavities are transversely partitioned by a plate resembling the pegma of younger riberiod rostronconchs. *Heraultipegma*, from the late Cambrian of France, has been regarded by some authors as the earliest rostronconch by virtue of the presence of a small pegma. A re-examination of additional material from the type locality reveals no consistent morphological feature that can be regarded unequivocally as a pegma of the sort possessed by riberiod rostronconchs. If *Heraultipegma* is therefore excluded from the Class Rostroconchia there remain no known fossils older than the New Zealand forms with characteristic rostronconch morphology. *Heraultipegma*, though not regarded as a rostronconch, is still considered to be an unusual kind of mollusc because of its distinctive morphology including a highly acicular skeletal fabric that is compatible with molluscan affinity (but not Arthropoda).

Also present are specimens of a tall-coned, moderately compressed univalve that is assigned to the Family Hypseloconidae. Although the overall shape of this form is reminiscent of early Plectronocerida (Cephalopoda) the absence of septation plus siphuncle precludes any close phylogenetic link between the two. Nevertheless, such an elongate form seems a plausible precephalopod ancestor occurring as it does in rocks only slightly older than the *Knightoconus* — bearing strata of Antarctica and perhaps 10 or 15 million years older than rocks containing the earliest known cephalopod, *Plectronoceras*.

Of particular interest are specimens of a bivalve with well developed dentition. Along the prominent hinge line there are four or five short, oblique bar-like teeth, both back and front, which converge ventrally toward the middle of the shell interior. An edentulous segment, located medially, may indicate a site of ligament attachment. On the basis of shell form and dentition this fossil is regarded as the earliest known representative of the subclass Palaeotaxodonta.

Filter feeding aspidobranch limpets from submarine thermal springs of the Galapagos Rift — A new superfamily of archaic archaeogastropods

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Numerous specimens of a new limpet were collected in early 1977 near vents of submarine thermal springs at a depth of 2,450m on the Galapagos Rift using the deep

submersible vessel ALVIN. They are conspicuous members of a previously unknown community of filter feeding animals that consume chemosynthetic sulphur-oxidizing bacteria.

The cap-shaped shell is composed of lamellar aragonite, has an irregular circular aperture with a maximum diameter of about 30mm, sculpture of fine radial ribs, and a fibrous periostracum that overhangs the edge. The protoconch is small, unsculptured; the first teleoconch whorl is smooth, has a deep suture and a prosocline lip; the next whorl is uncoiled. The shell muscle (and muscle scar) is relatively small, crescent-shaped, posterior to the apex, opening toward the left, enveloping the viscera but not the deep mantle cavity that extends along the entire left side. A low shell ridge originates on the columellar region of the early coiled phase and extends through 1/4 the arc of the muscle scar.

The neck of the animal is long, broad and deeply grooved along the left side. Eyes are lacking; cephalic tentacles are directed posteriorly. In males of all sizes the left tentacle, which lies in the inhalent side of the mantle cavity, is larger than the right. The foot has an anterior pedal mucous gland and a series of epipodial tentacles along the posterior and right posterior sides.

The single bipectinate gill is massive and is attached only on the ventral, efferent side; long filaments overhang the neck and reach a food groove on the dorsal right side of the neck. The food groove cuts diagonally toward the mouth, over the cephalic tentacle, not under it as in pectinibranch filter feeders. The feeding mechanism is evidently similar to, and convergent with, that of the mesogastropod family Calyptraeidae.

The radula is rhipidoglossate and is unlike any other known. Salivary glands are lacking; the intestine has a long anterior loop; the anus is directly over the neck. The gonad connects to the right kidney; in females the opening to the mantle cavity has a rosette-shaped lip, which is lacking in the males. None of the organs have the paired condition of zygobranch archaeogastropods. Unlike zygobranchs and trochaceans the heart is monotocardian and the rectum does not penetrate the ventricle. Efferent branchial and pallial veins enter the auricle at its posterior end.

A truly bipectinate ctenidium specialized for filter feeding has heretofore been unknown and considered unlikely. Paleontologists, however, have speculated that some extinct archeogastropods had to be filter feeders because the shells were too massive for the animal to be mobile. This new limpet demonstrates how a bipectinate ctenidium may be modified for filter feeding: filaments are lengthened and increased in number, afferent support is lost, and complete efferent attachment is necessary. The early coiled phase suggests that it is derived from coiled predecessors. I surmise that its affinity is with extinct groups in which the gill structure was very likely similar. In the classification of Knight and others (1960) it is placed in a new superfamily provisionally assigned to order Archaeogastropoda, suborder Macluritina.

The evolution of some higher taxa in gastropods

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Comments are confined to the possible evolution of gastropods from a procerithiacean stock which may represent a single line of descent from archaeogastropods and appears distinct from the *Littorina-Rissoa* taxa. The evolution of the procerithiaceans may have been related to the success of a high-spired gastropod living on a soft substratum, the habitat of Recent descendants. The superfamily Cerithiacea, pruned of families known to

have been placed there erroneously, is considered to include some of the most primitive living representatives. To these are related the strombids which have developed a remarkably extensile snout for probing soft substrata. This is followed by the development of the acrembolic proboscis capable of complete retraction and associated with flesh eating. It occurs in the sponge-feeders, triferids and cerithiopsids which retain the *Cerithium*-like shell, and the coelenterate feeders, mathildids, epitoniids and architectonicids in which prosobranch characters outweigh opisthobranch ones, and on this basis they are retained in the caenogastropods and not regarded as opisthobranch. The balance towards opisthobranchs is turned in pyramidellids in which the acrembolic proboscis is used for piercing and sucking animal tissues. No other evolutionary line of procaenogastropods has evolved a mosaic of opisthobranch-prosobranch characters and this is the main basis for suggesting that opisthobranchs have arisen from the procerithiaceans. It is proposed to subdivide the subclass Opisthobranchia into two superorders, the Pyramidellimorpha and Euopisthobranchomorpha, the origin of the pulmonates being close to the latter. We know of other gastropods which on the basis of certain characters must have had an origin close to that of the Euopisthobranchomorpha, these are the Omalogyridae and Rissoellidae which should undoubtedly be removed from the Rissoacea and raised to superfamily level.

The heterogastropods are not considered to be a valid group of gastropods, but a convenient descriptive term for those which may have followed some initial steps towards the opisthobranch grade.

Scar tactics of gastropods: predation and the fossil record

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Predation by means of crushing is an important cause of death for many gastropods, especially in shallow-water tropical environments. The increasing incidence of characters conferring resistance to crushing (strong sculpture, apertural teeth, slit-like apertures, etc.) since the middle Mesozoic suggests that the intensity of crushing has increased over the past 150 to 200 million years. In order to evaluate this hypothesis, the incidence of repair-marks on shells has been examined in fossil and Recent gastropods, and empirical relationships between the frequency of shell breakage in nature and incidence of shell repair are being derived. Preliminary data from Guam (Mariana Islands) and Majuro (Marshall Islands) suggest that there is a positive correlation between breakage and repair in at least three reef-flat gastropods (*Conus sponsalis*, *Rhinochlamys fasciata*, and *Strombus gibberulus*).

Reef-flat gastropods can be placed in three categories with respect to the incidence of repair. The first category contains species that have no significant escape in size from such crushing predators as crabs and fishes; repair in such species, which include small cerithiids, *Conus sponsalis*, and *Strombus gibberulus*, is rare. The second group of species is characterized by frequent shell repair; they have a distinct escape in size from crushing predators, but the structure of the lip is such that an attacker usually succeeds in chipping away part of the body whorl, so that the snail, must repair the injury. Examples include the larger cones, most species of *Rhinochlamys*, and all terebrids. The third category of species contains those with a strongly thickened lip which is rarely breached by an attacker once the gastropod has achieved a sufficiently large size; examples may include *Strombus mutabilis*, *Cerithium nodulosum*, and *Bursa bufonia*.

Food specialisation and the evolution of predatory gastropods

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Predatory prosobranch gastropods are an extremely diverse trophic group including some 26 families of meso- and neogastropods. A wide variety of prey types are consumed by the gastropods including most groups of larger invertebrates, and an array of specialised techniques has been evolved in order to catch, immobilise and extract the prey. Evidence is presented from studies of guilds of species in different tropical families that competition has been a major force in determining the food and habitat specialisations of the different predatory species. Similarly, over evolutionary time, competitive interactions may have resulted in the food and habitat specialisations of the different families. Most of the families of predatory gastropods appeared in a massive evolutionary radiation during the Late Cretaceous and evidence for the origin of the major groups will be reviewed. By comparison with living species the early predators from the Albian probably ate sedentary polychaetes and molluscs, whilst the more specialised families did not evolve until the Campanian and Maastrichtian stages. There was an exponential rise in the number of families and species until the Eocene, by which time it is probable that the main adaptive zones occupied by predatory gastropods had been largely filled. Evolution since then has consisted mainly of diversifications within the adaptive zones of particular families. The recent high diversity of food and habitat generalist species at high latitudes can be associated with the onset of polar cooling in the Late Miocene. The Turridae reached their present levels of high diversity during the Eocene and their relative importance at high latitude and in offshore habitats was established by the Lower Miocene.

Composition and origin of the molluscan fauna of the Tertiary of South Eastern Australia

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The Australian coastline has been divided into two regions based on the distribution of Mollusca and other marine invertebrates (Ekman, 1953; Wilson, 1971). These are the tropical Indo-Pacific faunal province and the Southern Australian faunal province. The latter has a unique temperate marine molluscan fauna with little in common with other regions and the molluscan fauna has for the most part its origin in the fauna of the Southeastern Australian Tertiary.

The Southeastern Australian Tertiary Mollusca fauna, part of which was first established in the Late Eocene, is composed, for the purposes of this discussion, of four elements (a) Australian — New Zealand, (b) Indo-Pacific, (c) Endemic and (d) Cosmopolitan. The proportions of the elements in the fauna fluctuated with time and during the Mid Tertiary the Indo-Pacific element was the largest because of an increase in migration of Indo-Pacific genera south when water temperatures rose. The Indo-Pacific element was much stronger in the western half of the South of the continent in the Eucla and St. Vincent Gulf

Basins from Early Miocene to Pliocene time and on the basis of this and other differences, two provinces have recognised in the Mid Late Tertiary, the Austral Indo-Pacific Province and the Southeastern Australian Province (Crespin, 1950; Ludbrook, 1969), the latter including the Murray, Otway, Bass and Gippsland Basins.

The fauna of the Southeastern Australian Province has been analysed in a manner similar to that done by Fleming (1967) for the New Zealand Tertiary, using similar criteria and the time ranges of 301 genera, thought to be representative of the fauna as a whole, have been plotted. Of these, 64 belong to the Australian-New Zealand element, 107 to the Indo-Pacific element, 86 to the Endemic element and 44 to the Cosmopolitan element.

Australian-New Zealand Element: Composed of genera common to Australia and New Zealand and not known to occur outside these regions. Fleming (1967) used the term Australian for this in his work. The proportion of the element in the fauna as a whole is about 29% in the Late Eocene, 32% in the Early Oligocene, then falling to 15% in the Pliocene and Pleistocene. In terms of actual numbers of genera present, there is a maximum of 49 in the Mid Miocene.

Indo-Pacific Element: The concept of this element is essentially that of Fleming (1967) and includes, in part, both the Present Indo-Pacific and Tethyan Eocene elements of handbook (1955). Examples of the later genera are *Orthochetus*, *Cypraedia*, *Ampullina*, *Sassia*, *Personella*, *Leptoscapa* and *Eocithera*.

The proportion of Indo-Pacific genera in the fauna as a whole is 25% in the Late Eocene, 21% in the Early Oligocene, rising to 34% in the Mid Miocene and remaining fairly constant in proportion (32%) through the Pliocene and Pleistocene. The maximum number of genera present is 76 in the Mid Miocene. Fleming's more thorough analysis gave about 100 genera in the Lower Miocene of New Zealand.

Southern Australian Endemic Element: This consists of genera not yet found outside the Southern Australian Region. In the Late Eocene it consisted of about 20% of the whole fauna but the proportion rises steadily with time to 36% in the Pliocene and Pleistocene. Absolute numbers are 20 in the Late Eocene, 68 in the Mid Miocene and 61 in the Pliocene and Pleistocene.

Cosmopolitan Element: These genera have a wide distribution through-out the world both in space and time. In the late Eocene they comprise about 27% of the fauna, drop to 14% in the Mid Miocene and rise to 17% in the Pliocene and Pleistocene. Absolute numbers of genera are, however, fairly uniform through the Tertiary at about 28 (22-32). Genera in this category are mostly bivalves.

The fluctuation of the proportions of the four biogeographic elements with time can be explained in terms of sea floor spreading and increase and decrease of sea water temperatures through the Tertiary. Following the splitting off of Australia from Antarctica in the Late Cretaceous, the Australian plate moved steadily northwards towards the tropics into the Indo-Pacific Realm. Increasing numbers of Indo-Pacific genera were therefore able to migrate into the Southern Australian region. In addition to the shift of the plate, sea water temperatures generally rose to a maximum in the Mid Tertiary, thereby allowing many Indo-Pacific genera to penetrate south. These genera gradually died out as water temperatures dropped. The greatest generic diversity is in the Mid Miocene when the effects of both the northward drift and increase in water temperatures were at their maximum.

In terms of proportions the Indo-Pacific and Endemic Elements have increased with time as the continent moved northwards at the expense of the Australian-New Zealand and Cosmopolitan Elements.

Functional interpretations of patterns in archaeogastropod radular morphology

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Morphological features of the complex rhipidoglossate radulae of marine archaeogastropods may be understood as consequences of interactions over evolutionary time of three major sets of constraints: phylogenetic, ecological and mechanical. Basic phylogenetic patterns have been identified in taxonomic research as constellations of associated characters that are conserved within families and genera. Ecological factors (notably substrate types and food sources) have led to specializations that have been superimposed repeatedly on basic phylogenetic patterns across the order. Scaling relationships and correlations between tooth dimensions and particle dimensions in deposits, on grazing surfaces, and in gut contents constitute strong implications, if not unequivocal demonstration, of ecologically superimposed adaptation.

Likewise, mechanical improvements that increase operating efficiency have been superimposed across the order, resulting in some striking examples of adaptive convergence. The basic movements of the odontophore and radula during feeding and the fundamental form of the rhipidoglossate radula form a conceptual biomechanical model that can be manipulated deductively to produce improvements in design. The predictive value of such analysis is confirmed by observations of actual configurations.

Six examples of mechanically significant patterns of adaptive convergence in rhipidoglossate radulae are discussed and illustrated in scanning electron micrographs and light micrographs. They are: (1) patterns of overlapping of tooth bases, shafts and cusps that transmit forces from one tooth to another; (2) patterns of interlocking elements within and between tooth rows to form joints that transmit forces in more complicated fashion, often involving a number of degrees of freedom; (3) losses of tooth shafts and blades coupled with modification of tooth bases to form specialized articulatory structures, particularly between the food-preparing and food-gathering portions of the radula; (4) structures related to load distribution on a single tooth, notably compressional ridges on the convex surfaces of tooth blades and those portions of tooth shafts where compressional forces are concentrated; (5) development of a pair of laterally situated, enlarged, primary food-preparing teeth per row in place of one centrally located primary food-preparing tooth; (6) development of radular asymmetry to accommodate enlarged food-preparing teeth when the radula is not in use and tightly folded.

Form, function and adaptive radiation in the Cerithiidae

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The family Cerithiidae comprises a large group of style-bearing prosobranchs in which sympatric genera and species are frequent. The family has undergone an elaborate adaptive radiation into various habitats. Adaptive peaks are seen in four major habitats: (1) subtidal

sand lagoons; (2) intertidal mud flats; (3) intertidal rubble flats; (4) high intertidal shores. The hypothesis is suggested that basic shell physiognomy, radular morphology, and anatomical features of the reproductive tract are directly correlated with substrate preference and trophic adaptation. The correlation of habitat with shell physiognomy can be demonstrated quantitatively.

Sexual strategies in Eulimidae (Prosobranchia)

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The family Eulimidae consists of a large number of species, most of which are parasites of echinoderms. They exhibit a very large variation in the way of parasitism and a still larger morphological variation, which is a result of their parasitic life. The most unmodified species retain all organ systems typical for mesogastropods, while some groups have lost almost all organ systems, except the reproductive organs and live as endoparasites. Some species live as ectoparasites only attached to their host by the proboscis and fall off as soon as the host is disturbed. Other species bury themselves in the body-wall of the host and/or form galls there. Some species live in the cloaca or in the coelomic cavity of the host.

I have met with the following sexual strategies in the family: (1) Gonochorists. (2) Protandric hermaphrodites. (3) Protandric hermaphrodites with environmental sex determination (ESD). (4) Simultaneous hermaphrodites (SH). (5) Specimens that start as females, turn to SH for a short time and then become females again. All species (except SH) exhibit a pronounced sexual dimorphism, with males of .1-.7 times the height of the females. ESD seems to be common.

The occurrence of sexual dimorphism may have two reasons: (1) To make it possible for the female to take out more energy from the host and thereby also increase the number of offspring of the male. (2) Reduce the predation on the male. (1) might be the reason in some cases when the parasite is big compared with the host, e.g. some parasites of ophiuroids. (2) is probably more often the reason because (1) can be excluded in most cases as the parasites occur in large numbers.

Gonochorists occur only among genera that have a comparatively weak association with the host, often leave it and associate with a new host. This will give the parasite numerous occasions to meet other specimens for mating. Gonochorism probably originates from primarily protandric conditions, because the species that have the most unmodified morphology are all protandric hermaphrodites. Another evidence is that all related families (Aclididae and Epitonidae) also exhibit some hermaphroditical traits.

The protandric hermaphrodites change sex at a certain size or age, not influenced by environmental conditions. They have a weak association with their hosts, but their biology is too poorly known to allow comparisons with other strategies.

The following type of ESD has been found in Eulimidae: The first specimen that settles on the host becomes a female, later specimens males. This usually results in groups with one female and two or three males. Sometimes males changes sex to females, presumably as a result of the disappearance of the female. This strategy will ensure presence of both sexes and reduce predation on the male phase.

The advantage of SH is striking for some species which form permanent associations with their hosts, because they use only a minor part of the ovotestis for sperm production. Other SH have a restricted mobility on their host and spend upwards half their ovotestis on sperm production. In this case, as also in (5), the biology of the species involved is too poorly known to see the advantages of the sexual strategy.

Commensalism of the cap limpet, *Hipponix conicus*

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The cap limpet, *Hipponix conicus* lives only on the shells of other molluscs. The cap limpet is believed to obtain food from its host mollusc, but the nature of this association has not been examined thoroughly. Using field manipulative experiments, this study investigated the degree of dependence of the cap limpet on its host, the benefits for the cap limpet involved in the association, and the effect of the cap limpet on the host.

Factors Influencing The Distribution of *Conus* in east Australian waters

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The distribution patterns of shallow-water species of the gastropod genus *Conus* in East Australian waters are presented. These patterns were determined from the results of numerical analysis of locality records of specimens in both museum and private collections.

Within the latitude range of the study (15°S-35°S) three bands of high faunal similarity can be distinguished. Faunal discontinuities occur around 25°S and 31°S and delimit each faunal band. The existence of these faunal discontinuities, and hence the distinct faunal bands, can be explained in terms of variations in local topographic complexity and water temperature.

The *Conus* fauna of areas between 15°S and 25°S is composed entirely of species typical of the Indo-West Pacific faunal region. A band of faunal overlap, characterised by a decrease in the number of tropical species and an increase in the number of temperate water species, exists between 25°S and 31°S. South of 31°S only temperate species have been recorded. The faunal discontinuity which occurs around 25°S, separating the tropical zone from the overlap zone, is strongly related to the southern extreme of the Great Barrier Reef. South of this discontinuity local topographic complexity is reduced and does not favour large communities of *Conus*. The southern faunal discontinuity (31°S) is closely related to the northern limit of movement of the 20°C surface water isotherm.

Within the overlap zone the species composition of the tropical component of the community is dynamic and suggests that a large proportion of this species group are species which have migrated into the overlap area each year. The possibility of such migration is enhanced in most tropical species of *Conus* by the inclusion of a pelagic phase within their larval development. Water circulation patterns in the Coral and Tasman Seas are complex and consequently it is difficult to determine the origin of migrant species. Undoubtedly the Great Barrier Reef is the primary source of larvae for the overlap area however isolated species records for both *Conus* and other molluscan genera indicate that larvae may enter the East Australian Region from New Caledonia.

The northern limit of the distribution of temperate species is obscure and requires further study especially in the light of the different reproductive strategies employed by this species group.

Comparative Anatomy of *Bulinus* and *Isidorella*

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The Australian planorbid genus *Isidorella* Tate, 1896 has at various times been synonymised with the African genus *Bulinus* Muller, 1781 and as a consequence included, along with *Indoplanorbis* Annandale and Prashad, 1920 in the sub-family Buliniinae. The diagnostic anatomical feature found exclusively in this sub-family is the ultrapenis which differs fundamentally from the normal planorbid copulatory organ.

Superficial examination of *Isidorella* and *Bulinus* indicates a degree of similarity belied by differences revealed in dissection. The salivary glands of *Bulinus* are tabular, passing through the circumoesophageal nerve ring and joining posteriorly. Those of *Isidorella* are flattened and branched where they lie on the buccal mass, and ribbon like where they pass through the nerve ring before joining. In *Bulinus* the insertion of the duct of the bursa copulatrix is on the proximal end of the vagina, whilst in *Isidorella* this duct is inserted at the distal end, almost at the female genital pore. The major difference is evident in the anatomy of the copulatory organ. *Isidorella* does not have an ultrapenis and consequently should not be placed in the Buliniinae. Its copulatory organ is a normal pendant penis, though two distinct forms are found in different taxa within the genus. In *Isidorella sisurnia* from Western Australia and the Northern Territory the penis has a simple duct opening laterally with lobed processes distal to the pore. This structure is also found in larger animals from Western Australia and western New South Wales. The other form of penis, probably derived from that just described, has no duct running down its length, but opens out just distal to the entrance of the vas deferens into two longitudinally folded spatulate processes covered with a prominent ciliated epithelium. This structure is found in *Isidorella brazieri* from the east coast.

The small northern species *oppletora jukesii* has been synonymised with *Isidorella* and consequently included in the sub-family Buliniinae. Dissection reveals that this species has a copulatory organ with a flagellum, the penis having a chitinised stylet. This structure is similar to the copulatory organ of *Physastra* and *Glyptophysa* and the affinities of *Oppletora* obviously lie here rather than with *Isidorella*.

The structure of the copulatory organ of *Isidorella* places the genus apart from all other planorbids, not only *Bulinus* and *Indoplanorbis*. The genus *Isidorella* should, therefore, be retained.

The distribution and biology of the freshwater gastropods *Physa* and *Physastra* in New Zealand

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Physastra (Planorbidae) and *Physa* (Physidae) are the only sinistrally coiled gastropod genera in New Zealand freshwaters. The former is represented by one, highly variable,

endemic species, *P. variabilis*, whereas at least one introduced species of *Physa* occurs. The commonest of these is almost certainly the European species *P. acuta*. *Physa* is widely distributed on both main islands of New Zealand in ditches, streams, lakes and ponds particularly close to urban areas and in agricultural areas or enriched water bodies. Its distribution resembles that of *P. (?) acuta* in South Africa where it has also been introduced recently. *P. variabilis* does not appear to be particularly common and occurs mainly in relatively undisturbed habitats including lakes and rivers. Comparisons with reliable distribution records from earlier this century indicate that *Physa* has replaced *P. variabilis* in many localities, for example in the rivers and streams around Christchurch. The two species are rarely found coexisting.

Growth and reproduction of both species has been studied in standardized laboratory conditions at water temperatures ranging from 6°C to 26°C. Growth rates of both species were similar (in terms of shell height increase) and snails attained similar maximum sizes. As has been found in other studies, snail density affected growth rate which was lower at higher densities. Fecundity of both species (eggs laid per unit time) also was similar but *Physa* reached reproductive maturity in half the time. The intrinsic rate of natural increase therefore is greater in *Physa* than *P. variabilis* and should enable it to build up large populations more rapidly.

In preliminary laboratory experiments, growth of *P. variabilis* was inhibited in the presence of *Physa* and all individuals died prematurely. However, when the species were kept apart by a nylon mesh screen which allowed free circulation of water, growth of *P. variabilis* was less inhibited and no snails died. This suggests that a form of interference competition occurred and further suggests that the geographic distribution of *P. variabilis* within New Zealand may have been reduced, at least in part, through competition with the competitively superior and more 'r-selected' *Physa*.

Freshwater gastropods of South Pacific Islands

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During 2 hydrobiological missions to South Pacific Islands in 1965 and 1971, the distribution of about 75 fresh — and brackish-water gastropods of different South Pacific Islands were studied (Southern East New Guinea and Long Island; New Britain, New Hebrides; New Caledonia; Fiji and Tahiti).

In the upper and middle courses in the mountains of the continental islands, species of Thiaridae such as *Melanoides (Melanoides)*, *Thiara* in eastern New Guinea or the endemic species of *Melanopsis*, further the endemic species of Hydrobiidae, such as *Heterocyclus*, *Hemistomia* and *Fluviopupa* in New Caledonia are characteristic. The last genus is also represented in Fiji and other western South Pacific Islands. In stagnant waters or streams with slow current are typically species of the genus *Physastra* (in New Guinea are also *Amerianna*, in New Caledonia also *Glyptophysa*) in the western Pacific islands. The number of the typically "inland-species" is diminished eastwards to the oceanic islands. On the transition of the middle to the lower courses of the running waters start the occurrence of the species of Neritidae with the genera *Neritina (Neritina)* and *Septaria*. This family is represented mainly in the lower courses with many species of *Neritina (Neritina) N. (Vittina)*, *N. (Neripteron)*, *Clithon*, *Septaria* and *Neritilia*. They occur, like the species of the subgenus *Stenomelania* of *Melanoides* (with freelifving veligers!), till the brackish zones of the mouth regions. These regions are influenced by the recurrent flow of sea-water during

high tide. The Neritidae of these brackish areas are associated with typically brackish forms such as the genera *Paludinella*, *Assimineia*, *Truncatella*, *Cassidula* and *Pythia*. Sometimes also marine species such as *Littorina scabra* are sporadic to find. With the recurrent flow also exclusively marine groups, such as the opisthobranchs, with the species *Strubiella paradoxa* (Acochlidiacea) is immigrated till the freshwater zone of isolated islands.

A remarkable hydrobiid fauna from Lord Howe Island (Gastropoda : Hydrobiidae)

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The Hydrobiidae of Lord Howe Island consists of 5 genera and 9 species. Three species have subspeciated, one into five subspecies and two into two subspecies. The total number of species group taxa is 5, more than on the eastern Australian mainland. It is suggested that this fauna is the result of 3 separate colonisations during the Pliocene and/or Pleistocene. Most of the species live in small streams but one is adapted to living on waterfalls and another is subterranean in habit.

One introduction was from eastern Australia and this group (*Fluvidona* Iredale) contains 3 species and also appears to have given rise to 2 new genera, one of them becoming subterranean in habit. *Fluviopupa* Pilsbry, an introduction from the north, has developed into 2 species which live sympatrically in some localities. The remaining genus group, tentatively referred to *Potamopyrgus* Stimpson, contains only one species which is found living on waterfalls.

Problems of dispersal and speciation in this fauna were discussed.

Reproductive systems in the Athoracophoridae

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Considerable differences exist in the arrangement of reproductive organs in the Athoracophoridae. Species vary in the amount of coiling of the oviducal gland, in the relative length of the oviduct, in spermathecal position, and particularly in the degree of fusion between the male and female tracts. The basic pattern is exemplified by *Triboniophorus graeffei*, in which the male and female tracts separate on leaving the fertilisation pocket, the oviducal gland is incorporated in the wall of the oviduct, and the prostatic gland is extended and lobular. In most New Zealand and subantarctic species a similar pattern is found, except that the oviducal gland is a distinct convoluted gland carried on one side of the oviduct, and the prostate is compact and discrete. In *Pseudaneitea ramsayi*, *Athoracophorus bitentaculatus* and *Palliopodex verrucosus* varying degrees of fusion of the male and female tracts are seen, with a diffuse prostate secreting at intervals into a male duct which forms a cleft in the wall of the female tract. It is considered that these three species evolved this condition independently.

Relationships within the family Rhytididae

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The Rhytididae is a large and complex family of carnivorous snails distributed from New Zealand and Australia, through the islands of the western Pacific with groups in the Seychelles and South Africa. The Australian fauna consists of about 27 species in 11 genera. These genera can be grouped with respect to shell, radula and anatomical characters into four or five groups. These can be compared with and notionally related to various non-Australian genera and groupings.

- Group I. *Victaphanta* — shell medium to large, almost smooth with almost no calcareous elements, umbilicus narrow to closed, radula of short, even lanceolate teeth, (40-60) — 1 — (40-60). Related to *Paryphanta*.
- Group II. *Prolesophanta*, *Saladelos*, *Echotruda*, *Tasmadelos* — shell small, smooth or with fine radial sculpture, radula of short, hook-shaped teeth to pegs, (14-26) — 1 — (14-26). Related to *Delos* and/or *Macrocycloides*.
- Group III *aphena*, *Strangesta*, *Namoitena*, *Occirhenea?* — shell small to large, with coarse, to fine radial sculpture and wide umbilicus, radula of grading lanceolate teeth, largest towards margin, (18-24) — 1 — (18-24). Related to *Ouagapia* and/or *Ptychorhytida*.
- Group IV. *Torresiropa* — shell small, carinate, radula not known. Possibly related to Group III.
- Group V. n. gen. for *capillacea* shell medium, wide umbilicus, sculpture of fine radial ribs, radulae with teeth grading to very large 9th or 10th tooth, (9-12) — 1 — (9-12). Related to *Rhytida* and possibly *Nata*.

Possible affinities of the genera in the family are discussed.

Patterns of Speciation in Camaenid Land Snails of the Kimberley, Western Australia

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Collections made by the author in the Pilbara and Kimberley areas of Western Australia in 1974, 1976, and 1977, together with materials in the Western Australian Museum, indicate a known fauna of about 150 species of camaenid land snails, two-thirds undescribed. Systematic revisions covering 75 species have been submitted to the Western Australian Museum for publication. These studies reveal that there are extensive alterations in the structures of both male and female terminal genitalia under conditions of congeneric sympatry. The terminal genitalia is used in species recognition by the snails. Also, there are quite different patterns of species distribution in several areas of the Kimberley. These differences suggest that speciation has occurred locally in different ways.

The Mitchell Plateau in the far northwest Kimberley is an elevated mound of bauxite bounded by big rivers and subject to a mean annual rainfall of 1,436mm (1968-1973), nearly all in November through March. It has a diverse representation of the camaenid land snail genus *Amplirhagada* Iredale, 1933 that show mosaic distribution patterns. Some species are restricted to the isolated islands of vine thickets, others tend to cluster among big boulders or talus in ravines, and one is widely distributed in the open eucalypt woodland. Species recognition is insured by major modifications in the male and/or female terminal genitalia. Aestivation site selection and strategy differ among species. Conchological similarities among species are many, but their ecology and anatomy differ dramatically.

The Napier Range inland from Derby is essentially a continuous high narrow limestone ridge running northwest to southeast that is periodically interrupted by either river gorges or strips of bare plains. Species of *Amplirhagada* show a leap-frog distribution, sometimes the shift occurring from one side of a gorge to the other, sometimes in as little as 100 meters of continuous and macroscopically uniform hillside. Some evidence of intergradation in a hybrid zone exists, and further fieldwork is planned in 1980 to study the contact zones between these closely related species.

The Ningbing Ranges, north of Kununurra and just west of the Northern Territory border, are broken up into short segments of narrow limestone ridges or a series of isolated limestone hills separated by alluvial plains and run almost directly north and south. Three genera are in linear replacement along the range, with the replacement areas not corresponding to major geographic gaps. Patterns of structural change under sympatry and local variation found in populations on neighboring hills indicate yet a third pattern of speciation in the Kimberley camaenids. The patterns of change outlined above are expected to be repeated in other groups of Kimberley camaenids and probably are applicable to Queensland and New South Wales camaenids.

A new order of interstitial, intertidal, systellommatophoran slug from Kaikoura, New Zealand based on a new genus and species (Mollusca : Systellommatophora)

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A new genus and species, the only known representative of a monotypic new systellommatophoran order is described. The new order is characterized by a stylommatophoran pulmonate type of reproductive system with male and female ducts opening via a common gonopore ventro-laterally on the right side behind the head, a posterior mantle cavity into which open the rectum, pneuostome and a renal papilla and in having the anterior fifth of the foot modified into a sucker. The head lacks tentacles and eyes, but the notum is modified on each side of the head into a pair of weak lappets.

The species lives interstitially between MHWN tide and MHWS tide zones on a steeply-sloping shore composed of polished limestone pebbles 1-2cm in diameter, at Rhino Horns Point, Kaikoura Peninsula, South Island, New Zealand.

The superorder Systellommatophora is elevated to subclass level the implication being that Pulmonata and Systellommatophora are parallel derivations from different types of opisthobranch ancestors.

The function of certain organs in the Opisthobranch family Gastropteridae

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The Gastropteridae is a family of specialized cephalaspidean opisthobranchs in which the parapodia are greatly developed into swimming organs, though this action is not confirmed for all species. Three genera, 18 species and 1 subspecies are attributed to the family. The animals are, in most instances, characterized by a specific positioning of various appendages on the visceral hump or on the posterior edges of the parapodia. The function of the appendages has not been previously explained.

The Gastropteridae, like other lower opisthobranchs (Cephalaspidea, Anaspidea), copulate in a head-to-tail fashion, the animal in front assuming the receptive female role, that behind the aggressive male role. Some lower opisthobranchs (aglajids, aplysiids) are renowned for their long chains of copulating animals. Such chains are readily accomplished among aggregations of slow-moving bottom-crawling species. In the flighty Gastropteridae, where often the slightest stimulus causes the animals to swim, successful mating involves not only penial penetration but also the ability of one partner to clasp the other.

Anatomical studies indicate two basic types of male organ in the Gastropteridae. In *Gastropteron rubrum* and other large species of that genus, and in *Sagaminopteron ornatum*, the male organ comprises a short to long cylindrical penial papilla within its atrium and a very long winding prostate gland. During mating, the penial papilla is wholly everted. In small species of *Gastropteron* with a mamilliform projection on the posterior face of the visceral hump, such as *G. cf. fuscum* from north-eastern Australia, the male organ is relatively much smaller, comprising two parts, the larger the atrium, short penial papilla and short prostate gland, the smaller an accessory organ of spherical bulb connected by a slender duct to the atrium. During copulation, the atrium, penial papilla and accessory organ evert to form a bifurcate penial organ with the prostate gland contained within the everted atrium.

In *G. cf. fuscum*, successful mating takes place in the following manner. Animal A senses and approaches animal B directly from behind. A distends its mouth-parts and sucks in the posterior projection of the visceral hump of B, apparently stimulating B to reduce its crawling rate and assume a quiescent receptive attitude. A contracts forward and everts its male organ. The larger part (the penis proper) pushes forward between the right parapodium and the visceral hump of B to the genital aperture below the gill. The smaller part (the accessory organ) loops round and fastens to the outer face of the right parapodium by means of minute hooks projecting from its partly introverted bulb. With this three-way hold on B, A is wholly prepared for any sudden evasive action by its partner due to outside stimuli, probably even remaining attached during swimming.

Among the larger species, *G. cf. bicornutum* from north-eastern Australia and *Enotopteron flavum* from the Yellow Sea have a peculiar spherical appendage attached to the rear edge of each parapodium. These species probably each have a long cylindrical papilla. Theoretically, it would appear that during copulation, the penial papilla of animal A passes between the right-hand spherical appendage and the visceral hump of animal B, stimulating B to tumesce its spherical appendage and so hold the penial papilla in position. The right-hand spherical appendage in these species is seen as the homologue of the accessory organ of small species of *Gastropteron*. Bilateral symmetry accounts for the presence of the left-hand spherical appendage.

Symbiotic chloroplasts in sacoglossans from south-eastern Australia

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The existence of actively photosynthesizing chloroplasts, without the rest of the alga, in the digestive gland cells of a number of species of the order Sacoglossa is now well known. Studies of sacoglossans from New South Wales have shown that while members of the family Elysiidae can maintain active chloroplasts in their tissues, members of other families of the Sacoglossa may retain pigment from their food plants, or even damaged but recognizable chloroplasts, but that these associations are not capable of photosynthesis. It is proposed that camouflage provided the initial advantage to the animals of retaining plastids in their tissues for some time before digesting them, and that the exploitation of the ability of the chloroplasts to continue to photosynthesize was a later development in the evolution of the association. Since *Elysia* spp. can maintain actively photosynthesizing chloroplasts for periods of months, while chloroplasts isolated from plant tissues in the laboratory will only photosynthesize for hours or at best for a few days, it is clear that complex physiological adaptations are involved in the maintenance of the chloroplasts within the animal cells. Recent studies have concentrated on the inter-relationships between photosynthesis by the symbiotic chloroplasts and respiration by the mitochondria of the animal cells.

Predator or prey : nudibranchs and coelenterates

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A close study is being made of the behaviour and associated body functioning of certain nudibranch species in relation to their coelenterate food. The principal subjects are the dendronotacean *Doto pita* Marcus and the aeolid *Cuthona reflexa* Miller. When searching for a place to settle the veliger seems unaffected by any contact with the tentacles of the thecate hydroid prey: the hydranths of the prey species *Obelia australis* and *Plumularia setacea* retract from the brushing action of the velar cirri and there is little or no nematocyst discharge. Final settlement and metamorphosis is mainly on the hydrocauli. Feeding on the hydroid tissue starts when *Doto* is c250µm long, and both the polyps and coenosarc are attacked. *Doto pita* is principally a suctorial feeder, though it will bite off the prey's tentacles. When *Doto pita* feeds on a polyp, the latter withdraws with little discharge of the nematocysts. In both nudibranch species fluid is actively expressed from the oral glands, the secretion being a mixture of mucus (much less viscid than that of the foot and body) and a protease: there is considerable external digestion of the prey. Suctorial feeding in *Doto* is effected by a pumping pharynx in concert with the periodic enlargement of the digestive cavity: in small *Cuthona reflexa* it is just by ceral movements. Large *Cuthona reflexa* bite off the hydranths. It does seem, though this study

does not provide conclusive proof, that the mucus reduces considerably the level of nematocyst discharge, outside and inside the nudibranch's body. There is no evidence of a binding function in the stomach, particles of prey circulating freely during the rest of digestion. A protective role for orally produced mucus seems supported by the method of feeding and gland structure shown by the main types of aeolid: the aeolidiids e.g. *Aeolidiella takanosimensis* Baba feed on sea anemones by a combination of dissolution, cutting and pulling, the huge composite oral glands producing mucus for protection and an enzyme for external digestion (dissolution); the glaucids (= facelinids) e.g. *Phidiana militaris* (Alder & Hancock) are rapid biters of hydrozoans, the scattered mucous glands of the oral tube and thick cuticle providing protection — there are no oral digestive glands.

Madreporarian coral and alcyonarian feeding by arminid and eolid opisthobranchs

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Records of opisthobranchs feeding on madreporarian corals are restricted to the aeolids *Phestilla melanobranchia* Bergh on *Tubastrea*, and *Phestilla lugubris* (Bergh, 1870) (= *P. sibogae* Bergh, 1905) on *Porites*. *P. lugubris* and three other opisthobranchs; 2 aeolids and one arminid, are reported living on *Porites* at Dar es Salaam, Tanzania. Adaptations to coral predation are shown in their life histories, ceratal structure and radular morphology. Similarities are suggested to be evidence of convergent evolution rather than close phylogenetic relationship.

Records of aeolid opisthobranchs feeding on alcyonarian or soft corals are also sparse, restricted to *Phyllodesmium* on *Xenia* and related soft corals. Two more species from East Africa and three from eastern Australia, are reported in this paper to be alcyonarian feeders. Ceratal structure and radular morphology are described and show interesting adaptations to their type of feeding.

Both the coral feeders and soft coral feeders are compared with aeolids feeding more normally on hydroids and sea anemones.

The zoogeography of thirty New South Wales opisthobranchs in relation to their larval development

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The zoogeography of thirty New South Wales opisthobranchs, from the three orders Bullomorpha, Nudibranchia and Sacoglossa, is discussed in relation to their mode of larval development. For the thirty species studied: twenty are planktotrophic; four are lecithotrophic; and six are direct developers. Except for eight of the thirty species, the

majority of them appear to have geographic ranges which are explainable in terms of their mode of development. Of those eight species, four are planktotrophic, one is lecithotrophic and three are direct developers. The indirect developing species with dispersal larvae, appear to be restricted to continental Australia. In contrast, the three direct developing species, with non-dispersal larvae, appear to be widespread (i.e. throughout the Tropical Pacific, Pacific, or Indo-West-Pacific). The biology and natural history of these eight species are virtually unknown to give any definite answers as to why these anomalies exist. Possible explanations are discussed which consider: (1) the taxonomic status of a few of these species; (2) the behaviour of the adults of species with non-dispersal larvae; (3) the ability of a species to vary its mode of development in different regions of its geographic range; and (4) some of the biotic and abiotic factors, other than development, which might influence the veliger larvae, causing them to have restricted distributions.

Ecology of sea hares (Aplysiidae) in the Leigh Marine Reserve, North Auckland, New Zealand

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A three-year study has been carried out on an intertidal population of the opisthobranch *Aplysia* (*Varrisa*) *dactylomela* Rang in Goat Island Bay, Leigh. The species is geared towards an extremely opportunistic life history with short (annual) generation times, high fecundity and long, continuous breeding seasons, high energy conversion efficiency and rapid growth rate. However at this situation *A. dactylomela* seldom has the occasion to exhibit these intrinsic properties. When the annual cycle, in terms of density at different levels across the shore, is followed and related to that of food algae (particularly three species of the rhodophycean genus *Laurencia* which serve as recruitment sites as well as food) it is found that this locality is marginal for the species. Winter storms exert the greatest toll of individuals (90%-95% mortality), but other simultaneous factors leading to the decline of the population are predation, decreasing availability of food and decreasing seawater temperatures. Although densities can be very high at times, it is shown that most individuals are reproductively immature and are likely to die before reproduction. This situation is contrasted with that for a subtidal population of another sea hare *Aplysia* (*Pruvotaplysia*) *parvula* Morch at the same locality. In this population the intrinsic properties of the species are more nearly realized by the individuals.

On the Dimyidae and Plicatulidae — proposed superfamily Plicatulacea

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The Plicatulidae have long been associated with the Spondyliidae in the superfamily Pectinacea. But resemblances are largely confined to cementation by the right valve, the monomyarian condition and, above all, by common possession of secondary, ball and

socket, hinge teeth. This last condition has now been shown to be connected with compression in the transverse plane of the primary ligament. But the Plicatulidae are alone in possessing a secondary (periostracal) ligament while the two differ profoundly in structure of the viscero-pedal mass. Thus both foot and frilled lips occur only in the Spondylidae, identical in these respects with the Pectinidae. Recent work on the Dimyidae⁴ (structure previously almost unknown) has abundantly confirmed earlier evidence^{2,3} indicating fundamental resemblances to the Plicatulidae. There is the same compression transversely of the primary ligament with an elongate dorsally running secondary ligament and some slight development of secondary teeth on an otherwise edentulous hinge. There is a similar absence of foot and frilled lips. As the name indicates, the Dimyidae have two (effectively three) adductors but the anterior one is reduced and conditions in the monomyarian. Plicatulidae may have evolved from something like those in the cemented Dimyidae whereas the Spondylidae clearly evolved with the Pectinidae from byssally attached ancestors. Other features in the Dimyidae, notably the reduced and functionless heart, the remarkably hypertrophied kidneys, loss of cerebropleural ganglia and absence of reflexion in the ctenidial filaments, are all probably associated with their small size and extreme lateral compression. It has been proposed^{2,3,4} that a new superfamily, the Plicatulacea (Dimyacea giving an erroneous impression of structure in the two constituent families) be erected to contain the Dimyidae and Plicatulidae.

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Mode of life and adaptive evolution in the cosmopolitan Triassic bivalve *Monotis*

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Monotis is a generally thin-shelled inequivalved inequilateral radially costate byssiferous bivalve occurring in large numbers in marine strata of Norian age in many parts of the world. Five subgenera have been erected to accommodate the 50-60 taxa covered: *Monotis* s.s. (medium size, subequivalved, fine ribs), *Eomonotis* (small; fine ribs, including on large posterior ear), *Entomonotis* (medium to large, coarse ribs, smaller, smooth ear), *Maorimonotis* (medium to large; thick shelled; coarse to obsolete ribs; reduced ears), *Inflatomonotis* (small; coarse ribs). Despite its abundance, widespread distribution and biostratigraphic importance few attempts have been made to understand its mode of life although some workers have suggested it was epi- or pseudoplanktonic or that it lived attached to seaweed.

Monotis occurs in virtually all marine lithologies but most commonly as shellbeds with fine sand to silt matrix. Its occurrence and morphology suggest it was generally attached throughout its postlarval life to a solid substrate in shallow marine areas with gentle currents

and low to moderate sedimentation rates. But there is no sign of the substrate to which it was attached.

This paper accepts the algal attachment theory and proposes that *Monotis* was epizoic on large algae comparable to modern kelp forests and that different morphotypes occupied different parts of the kelp-like plants and evolved to cope with slightly different environmental conditions. *Eomonotis* may have occupied distal portions of the laminae, with the larger *Entomonotis* on the stipe and less delicate laminae; morphologically aberrant *Maorimonotis* possibly became truly bottom dwelling and endobyssate. Periodic storms would tear some plants off the seafloor and these with their epifauna could drift off to other regions allowing *Eomonotis* and *Entomonotis* to achieve their wide distribution as accidentally pseudoplanktonic specimens, some of which continued to reproduce in their new habitat and establish new populations.

Thus evolution would have proceeded from a small, light, subequivalved, possibly epi- or pseudoplanktonic ancestor (e.g. *Otapiria*) to produce firstly *Eomonotis*, then by size increase and ribs coarsening to *Monotis* s.s. and *Entomonotis*, followed by weakening of sculpture and reduction of ears (*Maorimonotis*). Known stratigraphic and geographic ranges support these postulates.

The geography of littoral adaptation in bivalves

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Amongst the bivalves, a number of species occur intertidally. Some, such as the mussel *Mytilus edulis*, are conspicuous because of their epifaunal habit and relatively large size, but many, because of their life habit and/or small size, are much less obvious. To obtain some idea of the success of the bivalves in colonising the littoral zone, total numbers of species and numbers occurring intertidally were estimated.

The total number of bivalve species shows a geographical trend of increase with decrease in latitude. A similar trend is shown in the number of intertidal species. However, when the number of intertidal species is expressed as the proportion of the total fauna, trends are not so obvious or uniform. The proportion of littoral species ranges from 0 to about 47%. Lowest values are found at high latitudes and highest values at middle latitudes, Britain (47% intertidal) in the northern hemisphere and southern Chile (45% intertidal) in the southern. For most other areas the proportion ranges from 15 to 35%.

Values of up to 47% for the proportion of bivalve species which may be found intertidally suggests that, in some areas at least, the bivalves, as a class, have had considerable success in colonising the littoral zone. However, some of these species will be primarily sublittoral although capable of penetrating the littoral zone to a limited degree; others will be truly littoral in the sense that their distribution is mainly in the intertidal zone.

For many areas there is insufficient data to allow these two groups to be distinguished, but such information is available for the British bivalve fauna. It suggests that while 47% of species may be found intertidally, only 25% of these (i.e. about 11.7% of all species) can be considered as truly littoral. If the same relationship is true elsewhere, then for most parts of the world approximately 4-10% of the bivalve fauna can be said to be successfully littorally adapted.

Aspects of the ecology of the giant clams *Tridacna gigas* and *T. derasa*

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On the Great Barrier Reef extensive poaching of giant clam stocks by foreign fishing vessels has occurred for at least the last ten years. Information on catches, their composition and catch per unit effort data were obtained from arrested vessels which probably represent only a small proportion of the total "vessel visits" to the Great Barrier Reef. Surveys were made of "fished" and "unfished" reefs to determine densities of *Tridacna gigas* and *T. derasa*, the two largest and therefore preferred commercial species. Using this information an attempt has been made to assess the magnitude of poaching on existing giant clam populations.

Despite *T. gigas* and *T. derasa* being conspicuous members of the coral reef community surprisingly little is known of their biology and ecology. Several aspects of their ecology are being investigated in permanent study areas established on Michaelmas Reef near Cairns. In one area 2.7 ha, nearly 1,200 giant clams have been tagged, mapped and measured to provide data on habitat preferences and rates of growth, recruitment and natural mortality. Regular sampling of *T. gigas* is being undertaken to determine the reproductive cycle. A report on progress to date will be presented.

Aspects of the biology of *Octopus tetricus*

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O. tetricus is the commonest species of octopus occurring in the waters of south-west Australia. Aquarium studies of growth and food intake have shown that the species grows rapidly under conditions of excess food supply, reaching weights of 2 kg within 6 months. However the rate of growth is directly related to the food intake and it is unlikely that wild individuals achieve such rapid growth.

Males have functional spermatophores when they are about 100-150g in weight while females do not usually lay eggs until they are about 2 kg in weight. However females mate when they are about 500g and the sperm are stored until egg-laying. Females lay up to 700,000 eggs, larger females being more fecund. Embryonic development takes between 22 and 45 days, depending on temperature. The planktonic larvae are 2.5mm long at hatching while newly settled individuals are about 18mm. in total length and weight about 0.3g. Reproduction occurs throughout the year, although there is probably a peak in spring/summer. The lifespan of *O. tetricus* is thought to be about one year.

A quantitative examination of the benthic molluscs of Cockburn Sound, Western Australia

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Thirty stations in Cockburn Sound, Western Australia, were sampled in triplicate with a 0.1m² Van Veen grab. Molluscs were the dominant organisms, constituting 72.19% of all individuals and 89.56% of the biomass. An area of high density and biomass figures was found in the mideastern portion of the deep basin of the Sound. Densities and biomasses outside this area were substantially lower. A comparison of the present results for the central basin with samples made 20 years ago showed no obvious changes which could be attributed to pollution. The seagrass *Posidonia* has disappeared from the eastern shelf in the last 20 years but the causes of this are unknown. This change has been reflected in the molluscs found on the eastern shelf. Two dominant molluscs, *Musculista glaberrima* and *Dosinia incisa*, are recommended for any environmental monitoring programme which might be conducted in Cockburn Sound in the future.

Territoriality in limpets : manipulative experiments and energy budgets

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Territoriality in limpets is now well established and involves the defence of an algal food source against other herbivores, particularly other limpets. This paper is an analysis of the balance between the limpets' requirements and the yield obtainable from the defended area. The approach is two pronged: manipulative field experiments to test the role of limpets in maintaining algal "gardens", coupled with an energy budget approach to balance the energetic needs of the limpet against algal production.

Three examples will be discussed:

1. *Patella compressa* occurs only on the kelp *Ecklonia maxima*, and adults occur singly on the kelp stipe. Experiments show this pattern is maintained by territoriality. Production by the kelp stipe enormously exceeds the requirements of the limpet, so that limitation of food cannot be the reason for territoriality. It is suggested that territoriality minimises damage to the stipe by grazing, hence conserving the plant.
2. *Patella longicosta* defends patches of the alga *Ralfsia expansa*. Juveniles occur singly on the backs of the shells, feeding there on the encrusting *Ralfsia*, but larger animals develop home scars on the rock face, passing through an intermediate stage when they feed on encrusting coralline algae before establishing their own *Ralfsia* gardens. While *P. longicosta* feeds on the corallines, its body weight drops, ash content rises and calorific value and gonad weight declines, suggesting that the food source is inadequate. Experiments show

that territoriality is essential for the maintenance of the gardens. Production by *Ralfsia* closely balances the needs of *P. longicosta*, but declines higher on the shore to the point that it may limit the zonation of *P. longicosta*. Intertidally, more than 90% of *Ralfsia* is maintained in limpet gardens, and the activities of the limpet increase the survival rate and the productivity of *Ralfsia*.

3. *Patella cochlear* occurs in incredibly high densities (up to 1600.m²), juveniles only surviving if they settle on the shells of adults, so that they become stacked on top of each other. Spacing is regular, so that maximum distances are maintained between limpets. Heavy grazing prevents growth of all algae except for the encrusting *Lithophyllum* and a narrow fringe of red alga (*Gelidium micropterum* or *Herposiphonia*) around most of the limpets. Although gut contents comprise almost solely of *Lithophyllum*, production and energy content of this alga are so low that it cannot alone support the energetic needs of *P. cochlear*. The gardens of red algae thus seem vital for the densely packed *P. cochlear*, for although they form only a small fringe around each animal, their production and energy content are high. Limpets which lack gardens have a higher ash content, lower calorific value and lower reproductive output. Experiments show that *G. micropterum* is dependent on the limpet.

Patterns of vertical distribution of intertidal limpets in New South Wales

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During 1975-1978 a study was made of the population biology of a group of common intertidal limpets on shores in the vicinity of Sydney, N.S.W. This group included representatives from the families Fissurellidae, Acmaeidae, Patellidae and Siphonariidae. The two smallest acmaeid limpets are found in restricted habitats on generally sheltered shores; *Patelloida mimula* being found mainly on oyster shells, and *Patelloida mufria* being found on the shells of the intertidal trochid, *Austrocochlea constricta*. Seven species occur on open coastal platforms. *Notoacmea petterdi* is found only on vertical or sloping surfaces at the highest levels on the shore, and the fissurelid, *Montfortula rugosa*, is found only at the lowest regions of the intertidal, or in rock pools. The other five species have overlapping vertical distributions in mid-littoral regions of the shore. The factors influencing the observed patterns of distribution and abundance were investigated for each species, to determine to what extent these five species co-exist, and how such co-existence is maintained or prevented.

It was found that competition for a limited food supply did occur in midlittoral regions of the shore. Experiments involving the caging of limpets in various combinations of species and at various densities, showed that the patellid limpet, *Cellana tramoserica*, was the superior competitor. It was able to cause increased mortality of two acmaeid limpets, *Patelloida alticostata* and *P. latrigrigata*, and of the two siphonarian limpets, *Siphonaria denticulata* and *S. virgulata*.

Observations on the feeding biology of these limpets showed that *Cellana*, with its large docoglossan radula, was able to graze the surface of the rock more efficiently than the other species. Siphonarian limpets are primarily grazers of macroalgae and can only feed effectively when there is some form of algal turf available. In the presence of *Cellana*, such a turf never develops. The smaller acmaeid limpets, although they too feed on microalgae,

have radulae with much smaller teeth than *Cellana*, and apparently cannot get enough food when in the presence of *Cellana*.

Co-existence of the five species in mid-littoral regions of the shore is maintained by several mechanisms. These include the presence of refuges for the smaller species (e.g. *P. latistrigata* can feed effectively amongst barnacles, whereas *Cellana* cannot), behavioural adaptations (e.g. *Siphonaria* can feed on the algal turf that develops on the shells of *Cellana*), and a great deal of variability in the intensity of settlement of juvenile recruits from the plankton. This latter, random effect ensures that high densities of any one species are not attained over the entire shore, nor are they maintained over long periods of time.

Selective site segregation in *Patelloida* (*Chiazacmea*) *pygmaea* (Dunker) and *P. (C.) lampanicola* Habe on a Hong Kong shore

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Hitherto (though originally described as a separate species), *Patelloida* (*Chiazacmea*) *lampanicola* Habe has been regarded as a "form" of *P. (C.) pygmaea* (Dunker). The conical shape of the shell in the former was assumed to result from the settlement and growth of some individuals of the population upon shells of intertidal *Batillaria* (Potamididae).

This study analyses a population of limpets resident upon a small sand flat in Hong Kong and concludes that *P. (C.) lampanicola* Habe is distinct from *P. (C.) pygmaea* (Dunker). This is based upon differences in radula teeth structure, shell morphometrics and behaviour. This study has, moreover, further demonstrated that the earlier confusion surrounding these species results from a very nice example of selective site segregation or resource partitioning. *P. (C.) pygmaea* inhabits stones (in this region of its total range) embedded in the sand but can and occasionally does reside, up to a length of 4.2mm, upon *Batillaria* shells. Thereafter the flattened form of the limpet shell, on a round substrate presumably makes such individuals more susceptible to either predation or dislodgement. The high-coned *P. (C.) lampanicola*, on the other hand, almost exclusively colonises living *Batillaria* (particularly *B. zonalis*) shells, but can, with little or no significant alteration in form, also colonise stones. *P. (C.) lampanicola* has a positive behavioural response towards *Batillaria* and is clearly living in symbiotic association with the potamidid. The benefits accrued by both are discussed.

Thus, the limited hard shore niche of a primarily soft shore environment (both species are restricted by very low salinities) has been partitioned by these two limpets; one occupies the stones and oyster shells, the other the dense cover of epifaunal potamid snails.

Competition and stability in a guild of limpets

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The Acmaeid limpet *Notoacmea onychitis* co-exists with the pulmonate limpet *Siphonaria kurracheensis* on a vertical rocky shores at Rottneest Island, Western Australia. Experiments in which the relative abundance of these limpets in replicate subpopulations were altered revealed features of the dynamics of the interactions between the limpets.

1. The composition of unaltered control subpopulation changes with time apparently due to yearly differences in recruitment. *Siphonaria* colonizes vacant areas; *Notoacmea* can invade occupied areas.

2. Each species shows evidence of population regulation in which members of the same species affect changes in numbers more than members of the other species, and *Notoacmea* affects *Siphonaria* more than the reverse.

3. The variability in the composition of experimental subpopulations compared to the mean composition of the control subpopulation decreased to pre-manipulation levels after 36 months.

These results add support to the idea that *Notoacmea* is a superior competitor on parts of vertical shore, but indicate that adjustments to disturbances of relative abundances take a relatively long time of three years.

Life-history strategies of five species of intertidal limpet

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The life-history strategies of five species of intertidal limpet, *Cellana tramoserica*, *Notoacmea petterdi*, *Patella peroni*, *Patelloida alticostata*, and *Siphonaria diemenensis*, which occur on the same shore but in different tidal zones, are considered in relation to their different environments. Attention is focussed upon reproductive effort, which is defined as the percentage of assimilated energy devoted to reproduction, and which is measured for each species by using annual energy budgets.

Interspecific differences in reproductive effort appear to be correlated with interspecific differences in rates of extrinsic adult mortality.

Experimental studies of the reproductive strategies of populations of the intertidal limpet *Siphonaria kurracheensis*

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Variations in life history characteristics have been shown to occur between populations of the same species of animals or plants living in different environments. One way of testing if these differences are fixed or plastic is to do reciprocal transplants of populations between environments.

I recorded growth, mortality, total egg output and duration of the breeding season for low and high shore individuals of the pulmonate limpet, *Siphonaria kurracheensis* on both a horizontal and vertical intertidal shore on Rottnest Is., W.A. One year after reciprocally transplanting animals between high and low shore I measured these characteristics.

On both shores I found low populations have a longer breeding season and lower average egg output per individual than high populations. Transplanted animals assumed the same breeding period as animals at the level to which they were transplanted. On the horizontal shore transplanted limpets also changed their average egg output to that of animals already at that level on the shore.

Growth and mortality were not significantly different between low and high populations on the horizontal shore. Low shore animals however grew more during the non-breeding time than the breeding season and experienced higher mortalities during the breeding season than the non-breeding time.

On the vertical shore low animals had a higher mortality during the breeding season than high animals and low shore animals grew more and died more during breeding than non-breeding times. Transplanted animals assumed mortality patterns of animals already at that level on the shore.

Therefore horizontal shore limpets showed differences in reproductive characteristics between low and high populations and these differences were plastic. Vertical shore animals showed differences in both reproductive characteristics and mortalities of low and high shore animals. High shore limpets were plastic in these characteristics but low shore limpets were not.

The influence of grazing by subtidal gastropods on the establishment of furoid algae

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Subtidal reefs in northern New Zealand may support high densities of herbivorous gastropods. These include a limpet *Cellana stellifera*, a turbinid *Cookia sulcata* and a trochid *Trochus viridis*. *Cellana*, *Trochus* and juvenile *Cookia* occupy a range of habitats

but are most abundant on bare rock flats in waters 3-12m in depth. In this habitat their abundance is positively correlated with that of the echinoid *Evechinus chloroticus* which by cleaning macroscopic algae from rock surfaces appears to provide suitable grazing sites for the gastropods.

Field experiments show that mixtures of the above gastropod species may prevent the re-establishment of macroscopic algae in areas from which echinoids have been removed. This paper outlines experiments in which the gastropods are enclosed separately to check the grazing influence of the different species. The results suggest that the grazing activities of *Cellana* and *Trochus* may enhance the establishment of a furoid alga *Sargassum sinclarii*, perhaps by removing ephemerals such as *Ulva*. However, the results are complicated by a caging effect which appears to be independent of the gastropod grazing. General ideas of gastropod grazing will be discussed in the light of these experiments.

The role of grazing by gastropods in the structure of intertidal communities

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On rocky shores in New South Wales there is usually a very abrupt upper limit to distribution of foliose macroalgae. Below this level, in most areas, algae occupy the entire surface of the rocks. Above this level, there are encrusting macroalgae on dry surfaces, foliose algae in pools and some small foliose algae between barnacles. Experiments are described to distinguish between the effects of physical factors (e.g. heat, light) associated with emersion at higher levels on the shore and the effects of grazing gastropods on the upper limit of distribution of algae. Grazing of algal spores by prosobranch gastropods determines the upper limit of foliose algae on the shore. Physical factors determine the biomass of algae in ungrazed areas. The lower limit of microalgal grazers (e.g. the limpet *Cellana tramoserica*) is determined by their inability to feed on macroalgae at lower levels on the shore. The effects of macroalgal grazers (the pulmonate limpets, *Siphonaria* spp.) and of rock-pools are also discussed.

Factors affecting feeding rates of the intertidal carnivorous gastropod *Morula marginalba*

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The intertidal whelk *Morula marginalba* has a more limited distribution than its prey with respect to both height on the shore and intensity of wave action. This is discussed in

relation to the effect of these factors on the rate at which *Morula* kills and eats the barnacle *Tesseropora rosea*.

Study of a tagged natural population of *Morula* provides evidence for seasonal shell growth by this species. Laboratory experiments are described which test for an effect of temperature on *Morula* feeding rate, and for an effect of season on the relationship between feeding rate and temperature. It is suggested that the results of these experiments account, at least in part, for the observed seasonality of growth.

To determine whether there is any basis for expecting *Morula* density to be positively correlated with prey density, field measurements were made on the effect of prey density on the feeding rate of *Morula* on adults and juveniles of a number of prey species. Concurrently with the above experiment, variations in feeding rates were observed in relation to the fortnightly tidal cycle.

The above results are discussed with respect to *Morula* sheltering behaviour and a model of *Morula* distribution is suggested.

A population model of the whelk *Thais orbita*

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A population model of the whelk *Thais orbita* at Fishhook Bay, Rottnest Island in Western Australia has been developed. Data on reproduction, recruitment, growth and mortality were considered in the model. Validation of the model by an experimental manipulation of the population at Fishhook Bay has been attempted. The results of the simulation and their significance will be discussed.

Shore-level size-gradients in *Thais* spp.

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Average body sizes in a variety of marine animals have been reported to be correlated with height in the intertidal zone. However, observations on four species of *Thais* show that the relationship between size-distribution and height (or depth) is highly variable. Intertidal size-gradients in *Thais* have been explained by a size-dependent set of responses to light and gravity, but cage experiments indicate that snails of different sizes behave similarly. It is argued that size-gradients are produced by the direct responses of snails to factors such as shelter, temperature, desiccation and food, and it is suggested that a response to 'token stimuli' is unlikely to evolve when the token stimuli are poorly correlated with the relevant environmental factors, especially if the latter can be monitored directly by the animal.

Food related reproductive strategies in different populations of *Nassarius pauperatus*

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Adjacent populations of *Nassarius pauperatus* differ significantly in how hungry their members are. Females from very hungry populations produce more eggs and egg capsules, but less eggs per capsule, than those from less hungry populations. It was hypothesised that these differences were related to food availability and this was confirmed in a laboratory experiment using two groups from the same population.

Adult mortality and cannibalism of egg capsules are known to increase as food availability decreases and the different reproductive responses to food availability are explainable in terms of these changes. A general hypothesis is also proposed from this work, relating reproductive strategies to dispersive ability.

ABSTRACTS OF POSTERS

On the life-cycle of *Velacumantus australis* (Gastropoda : Potamididae) in the Swan estuary, Western Australia

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Velacumantus australis is the intermediate host of the avian schistosome *Austroilharzia terrigalensis* in the Swan estuary, Western Australia, and aspects of its ecology are being studied as part of an investigation into the epidemiology of this parasite. The longitudinal and vertical distribution patterns of *V. australis* are associated with that of the macrophyte *Halophila ovalis*. *V. australis* is found from the shallows to a depth of approximately 6m but attains its greatest population density between 0.5 and 1.75m. Changes in growth, maturation and population density were documented from monthly, quantitative samples and related to the prevailing temperature and salinity regimes. A generation hatching during the 1976/77 summer grew rapidly until May 1978 when lengthwise growth stopped and did not resume until late spring. The progress of oogenesis and spermatogenesis was assessed from the increasing diameter of developing oocytes, the development of spermatozoa and the changes in the diameter of ovarian and testicular tubules. Gametogenesis corresponded more closely to the rising spring temperature regime than to seasonal fluctuations in salinity. The first evidence of gametogenesis was found in July (\pm 17 months after hatching). The first spermatozoa were found in October 1978 and by November the largest oocytes had attained a diameter of approximately 160 μm . *V. australis* lives for about 2½ years, breeding during its second summer.

Infection by larval trematodes either obliterates or greatly reduces gonad development. The prevalence of infection increases upstream and near the upstream limit of its distribution in the estuary, up to 67% of the *V. australis* population may be infected.

Studies of muscle metabolism in the marine bivalve mollusc *Tapes watlingi*

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Many studies of the composition of biological tissue and of metabolic reactions therein are hampered by the need to disrupt the tissue in order to identify and quantitate the various metabolites. In recent years nuclear magnetic resonance (NMR) spectroscopy has provided a means of overcoming this problem by virtue of its ability to observe metabolites in intact tissue. Natural-abundance ^{31}P NMR spectroscopy is particularly useful in this respect because it allows the observation of the major phosphorous-containing metabolites, many of which play a central role in metabolism and bioenergetics.

We have examined excised foot and adductor muscle and whole hearts from the marine bivalve mollusc *Tapes watlingi* (the "tapestry cockle") by ^{31}P NMR spectroscopy. The spectra of healthy tissue show prominent resonances from arginine phosphate, AMP, ADP, ATP, sugar phosphates and inorganic phosphates. The fate of these metabolites during tissue ageing has been examined under aerobic and anaerobic conditions and in the presence of various metabolic inhibitors. The position of the inorganic phosphate resonance provides a sensitive monitor of tissue pH. The results of these studies will be compared with similar studies on terrestrial vertebrate tissue.

Energy metabolism of the heart of the mollusc *Tapes watlingi*

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Metabolic inhibitors, anoxia and measurement of oxygen consumption have been used to study the energy metabolism associated with the contractile process of the isolated heart of the bivalve mollusc, *Tapes watlingi*. In this tissue oxidative phosphorylation is used as an energy source for spontaneous contractions, however, if oxygen is removed the tissue is able to metabolise anaerobically and thus maintain near optimal activity. Glycolysis is important in maintaining energy demands for contraction of *T. watlingi* heart, since in aerated medium and in the presence of glycolytic inhibitors the activity gradually decreases to about half the control value. The mollusc heart is more adaptable than mammalian tissue in utilizing alternate metabolic pathways to maintain energy production.

Aspects of the biology of *Gazameda gunni*
(Reeve, 1849) a viviparous mesogastropod and
potential "indicator" of perturbation induced by
sewage pollution.

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Gazameda gunni has a wide distribution on the Continental Shelf off Sydney, N.S.W. inhabiting sandy mud from 55 to 135 metres, with abundance directly related to sand grain size, clay and gravel content of the sediment. *Gazameda gunni* feeds on phytoplankton using specialised ciliary currents and sorting mechanisms which are a modification of the three basic types previously documented for ciliary feeding prosobranchs. The specialised mode of feeding is believed to be related to the brooding of large eggs.

The reproductive system is similar to that of *Turritella communis* in that it consists of an open pallial oviduct. It has, however, a specialised brood pouch which separates the ctenidial complex from the mantle floor. Furthermore, the male reproductive system is similar to that of *Turritella communis*, except that *G. gunni* is a proterandrous hermaphrodite in which the male phase undergoes a brief sexual change which has both male and female anatomical structures. Subsequent to this hermaphroditic phase a female begins and lasts throughout the remaining life. All females in populations of *G. gunni* are reproductively mature.

Embryos are brooded within a brood pouch as an embryonic mass held together by a cylindrical sheath which is attached to the posterior end of the mantle cavity. The egg size at oviposition is relatively large (0.96-1.00mm) compared to other gastropods.

Brooding lasts for a relatively long period (approx. 200 days) until embryos reach 2.6-3.0mm in size and are released as crawling juveniles. The period of development is the longest recorded for a prosobranch.

Oviposition occurs during January in *G. gunni*. The release of metamorphosed juveniles of *G. gunni* occurs during the maximum availability of phytoplankton (August-January) in these waters. It would be advantageous to release juveniles at this period as brooding of large eggs would interfere with feeding.

A significant ($p(0.005)$) linear regression was found between the numbers of eggs and shell size which shows that larger individuals have larger clutches. No relationship was found to exist between shell length and size of eggs, indicating that egg size is constant over size (age).

Quantitative evidence suggests that an increasing gradient of pollution is associated with small egg and clutch size in *G. gunni*. Sewage pollution may reduce the production of oocytes in *G. gunni* by inhibiting feeding by clogging ctenidia.

The reproductive tactic of brooding with a long time of prehatching development is advantageous in that prehatching mortality is nearly non-existent. However, producing a large number of offspring of dispersive type larvae would be advantageous to a local population under conditions of high juvenile mortality induced through environmental stress. Longevity is shortened at polluted sites and this could contribute to local population extinction due to reduction of the number of oocytes produced per female. Further investigation of life history phenomena may show that pollution could greatly increase the

chance of extinction of a local population of *G. gunni* by "interference" with life history tactics. This investigation suggests that a change of reproductive mode or "switch" (e.g. *Crepidula*) is non-adaptive in a local population of *G. gunni* where there is sewage pollution.

Unveiling Australian Ovulids

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Part 1:

A photographic essay establishing how specific living animal patterns and colours of Australian ovulids are true to each species and can be utilised to determine field identification.

Part 2:

Relationships between ovulids and their host alcyonarians, specific or non-specific?

Part 3:

The taxonomic determination of ovulid species utilising radular characteristics, known variations in shell features and geographical distribution.

Multiple haemoglobins in arcid clams

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Many arcid clams possess erythrocytic haemoglobins. The following species of arcids were collected from the waters of Australia and the near Indopacific; *Anadara trapezia* (Deshayes), *Potiarca pilula* (Reeve), *Scapharca gubernaculum* (Reeve), *Tegillarca granosa* (Linne), *Anadara antiquata* (Linne), *Anadara nugax* Iredale and *Anadara passa* Iredale. Their haemoglobins were examined by electrophoresis. Each species possessed two haemoglobins which were present in species specific patterns. The two haemoglobins in each species are genetically controlled at two different loci.

In *Anadara trapezia* a genic polymorphism is displayed by one of the haemoglobins (Hb-2). The usual alleles are Hb-2a and Hb-2b. This polymorphism was present in all of the thirty populations of *A. trapezia* studied. The haemoglobin gene frequencies formed a complex cline; Hb-2a was more common at lower latitudes than Hb-2b which was prevalent at higher latitudes. The oxygen equilibrium curves of Hb-2a and Hb-2b, prepared from homozygous individuals, and Hb-2a + Hb-2b, prepared from heterozygotes, were determined at 15, 20 and 25°C. The curve of Hb-2a was consistently to the right of that of Hb-2b. The curve of the heterozygote was between those of the two homozygotes at 15 and 20°C but at 25°C was almost coincidental with that of the Hb-2a homozygote. This means that at a given temperature animals homozygous for Hb-2a can deliver more oxygen to the tissues for the same amount of cardiac work than can those homozygous for Hb-2b. The advantages of this

to animals living at low latitudes become apparent when it is remembered that the oxygen capacity of water decreases with increasing temperature. Studies on the interaction coefficients of the haemoglobins suggest that the heterozygote has an advantage over both homozygotes at high temperatures.

The lack of polymorphism in the other arcids which were examined is probably related to the relatively stable water temperatures which occur in the tropics for *A. trapezia* was the only species examined whose distribution extends into the cool-temperature region.

Aspects of the biology of *Idiosepius notoides* (Mollusca : Cephalopoda)

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Idiosepius notoides Berry is a small sepioid cephalopod found in the seagrass beds of the Sydney region. It is likely that its distribution extends over much of Australia's subtropical coastline coinciding with the presence of the seagrass beds.

The species is sexually dimorphic and is easily distinguished by its small size and the rugose pad on the surface of the mantle. This pad is used for attachment to the seagrass blades.

Specimens are collected from Careel Bay at monthly intervals, using a fine mesh beam trawl. After fixation in 5% formyl-seawater the animals are sexed, measured and weighed.

Analysis of these data indicates that *I. notoides* is an annual species with a prolonged breeding season extending over the summer months (Oct.-Jan.).

Growth of *Haliotis ruber* in N.S.W.

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A commercial fishery for the blacklip abalone, *Haliotis ruber*, in New South Wales currently yields approximately 400 tonnes of abalone valued at A\$750,000. A program of research aimed at determining appropriate yields for the fishery includes the tagging of abalone to determine growth rates.

Abalone were tagged at 13 sites near 4 major ports, with numbered plastic tags and cyanoacrylate glue. Recoveries to January 1979 numbered 742 representing a recovery rate of 13.5%. Time at liberty varied from 4 weeks to 108 weeks and lengths at recapture varied from 22mm to 133mm.

Recapture data were fitted to the von Bertalanffy growth equation, $L_t = L_{\infty} [1 - \exp(-Kt)]$ where L_t = length at time t .

L_{∞} = average length at which growth ceases

K = rate at which length approaches L_{∞}

The data were fitted using the Fabens method.

Loo's varied from 115mm to 141mm and the respective K values varied from 0.35 to 0.24. Parameters currently being used for yield analysis are $K = 0.43$, $L_{\infty} = 136\text{mm}$.

136mm is less than the mean length in very lightly fished populations and further work is needed to resolve this anomaly. Other work being undertaken includes natural mortality and reef productivity investigations.

Occurrence of interstitial and opisthobranch molluscs on Fijian coral reefs

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Collections of opisthobranchs have been made at five stations from coral reef habitats on Viti Levu. All areas investigated were accessible at low tide by turning chunks of coral or snorkelling over the reef.

Interstitial molluscs recorded from Fiji for the first time include representatives of the order Nudibranchia (*Pseudovermis* sp., *Embletonia* sp.) order Acochliidae (*Hedylopsis* sp., *Microhedyle*) and one species of Soleonogaster. The major habitat of the interstitial molluscs is coarse sand pockets on the reef where there is always standing water in the pools and where there is abundant water flow from surge or during tidal change. Another suitable substratum occurs behind the fringing reefs near shore where coarse coral sand is constantly moved by wave action from breaks in the reef or across the reef lagoon.

Larger opisthobranchs including representatives of the orders Nudibranchia, Cephalaspidea, Anaspidea, Notaspidea and Sacoglossa were most commonly found under chunks of dead coral either in small pools near the edge of the reef at low tide or in the rubble zone. They were associated with encrusting growths of hydroids, sponges, algae and bryozoans which are undoubtedly their food sources. Other species appear to live in the reef crevices, as evidenced by the large numbers of crawling forms found on the reef at night.

Species are usually found as single individuals or a low number in any one collection. However, after numerous collections, it is evident that there are common and rare species on the reefs.

Cephalic brood pouches in *Planaxis* and *Fossarus* (Fossaridae and Planaxidae, Cerithiacea, Gastropoda)

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Both *Planaxis sulcata* (Born) and *Fossarus* spp. have a large cephalic brood pouch in the haemocoel in the posterior part of the head. In both genera the pouch appears to be formed

by an epithelial invagination. Its opening to the exterior is a small, slit-like aperture adjacent to the anterior end of the pallial oviduct. Fertilized eggs are deposited in the brood pouch and undergo development to at least the late veliger stage.

The existence of strikingly similar brood pouches in the Planaxidae and Fossaridae suggests that they may have a closer relationship to one another than previously suspected. The freshwater Thiaridae also have a cephalic brood pouch but, unlike the Planaxidae, are parthenogenic.

Stress in estuarine molluscs as measured by adenylate energy charge

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The stress associated with reduced salinity in the gastropod *Pyrazus ebeninus* and the bivalves *Anadara trapezia* and *Saccostrea commercialis* was measured by the adenylate energy charge technique. A statistically significant fall in energy charge occurred in all species when salinity was reduced from 35‰ to 10‰. Mean energy charge values for animals in the low salinity conditions (10‰) were 0.61 for *P. ebeninus*, 0.69 for *A. trapezia* and 0.53 for *S. commercialis*, compared with mean energy charge values in the control animals (35‰) of 0.85 — 0.87 for *P. ebeninus*, 0.84 — 0.85 for *A. trapezia* and 0.64 — 0.76 for *S. commercialis*. The decrease in energy charge occurred within 24h; no further change was found with exposure to low salinity for 48h (*A. trapezia*) or 120h (*P. ebeninus*, *S. commercialis*).

The reduction in energy charge in the three molluscs may have been associated with reliance on anaerobiosis as an indirect result of reduced salinity and, as such, may reflect their relative ability in an unfavourable environment to reduce metabolic demand while using anaerobic processes.

These results were used to examine the value of adenylate energy charge as a biological indicator of the severity of departure from normal environmental conditions.

The genus *Tricolia* (Archaeogastropoda: Phasianellidae) in Australia

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Australian species of *Tricolia* Risso, 1826, have mainly been grouped in the genus *Pellax* Finlay, 1927, but Ponder (1965) has shown that the type-species of the latter is a mesogastropod (an eatoniellid) and is thus unrelated.

There are six species of *Tricolia* in Australia, four of them endemic. Judging by shell and radular characters, the Australian species closest to *Tricolia*, s.s., of Europe is *T. fordiana*

(Pilsbry, 1888), which ranges from the Persian Gulf to Western Australia and Queensland (it has not yet been recorded in the literature from Australia but is an abundant minute species). *T. tomlini* (Gatliff & Gabriel, 1921) is a southwestern Australian endemic, while *T. gabiniana* (Cotton & Godfrey, 1938) is endemic to southwestern and southern Australia (east to South Australia). In life, both commonly have a bryozoan epizoic on the shell. *T. rosea* (Angas, 1867) is endemic to all of southern Australia. Judging by its large first shell whorl and the enlarged aperture of the presumed female, there may be ovoviviparity. *T. tomlini* and *T. rosea* have radulae with a narrow central tooth between the two innermost laterals. In the subgenus *Hilola* Pilsbry, 1917, this trend leads to fusion of the innermost pair of laterals into a pseudocentral. *Hilola* has both shells and radulae that are sexually dimorphic, and in Australia is represented by *T. (H.) virgo* (Angas, 1867) in New South Wales and Western Australia, and *T. (H.) variabilis* (Pease, 1860-61), a widespread Indo-Pacific species occurring in Queensland (not yet recorded in the literature).

Pellax johnstoni Cotton, 1945, of southwestern Australia, may be a true *Pellax*.

A major conclusion of the study (which considers all the Indo-Pacific species) is that the shell features of *Tricolia* are evolutionarily conservative while the radulae are plastic. Erection of subgenera and genera based solely on radular characters is therefore not advised. Studies of the living animals are much needed.

Embryology of three N.S.W. Opisthobranchia

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A poster display will depict the major embryonic events in the development of three nudibranchs. Each species will represent one of the three types of development found among local fauna. Planktotrophic development (Type 1) will be represented by *Dendrodoris nigra*. For this species two larval forms will be shown. Lecithotrophic development (Type 2) will be illustrated by *Hoplodoris nodulosa* and direct development (Type 3) will be represented by *Rostanga arbutus*.

On the ultrastructure and histochemistry of the digestive gland of *Oncomelania hupensis quadrasi* (Hydrobiidae)

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This amphibious prosobranch from the Phillipines is an intermediate host of the human schistosome, *Schistosoma japonicum*. The parasite matures in the connective tissue and haemocoelic spaces around the digestive gland of the snail. An examination of the

ultrastructure of the digestive tissue of healthy, uninfected snails has been undertaken prior to investigation of the effects of parasitism on the gland.

The digestive gland of *O. h. quadrasi* occupies the posterior region of the visceral mass, where it is mingled with the gonad. It consists of two unequal lobes of a compound tubular or acinar nature, connected to the stomach by a central duct which opens near the oesophageal entrance.

The gland ducts are lined with a columnar ciliated epithelium, whilst the lobules of the gland consist of three types of cells here described as the digestive cell, the secretory cell and the narrow cell. In previous light microscope studies of prosobranchs these three types have been described and in some cases a fourth type, the calciferous cell, was reported. Work on pulmonates also described a mucous cell, which has not been found in prosobranchs.

The digestive cell is a columnar cell which appears to go through various morphological changes throughout its life. It has a dense brush border of microvilli along the apex, which assists in its main function, the absorption and digestion of food material from the lumen of the gland. The characteristic appearance of organelles such as the poorly developed Golgi apparatus and endoplasmic reticulum and small dense mitochondria, can be seen at all functional stages of the cell.

The secretory cell is conical in shape and is characterized by a well developed granular endoplasmic reticulum and Golgi apparatus involved in the production of zymogen granules. Most secretory cells in addition contain an electron dense aggregate that, by means of electron microprobe analysis, has been shown to contain calcium. This dense aggregate is eventually released into the lumen of the gland. The secretory cell in *Oncomelania* therefore combines, to some extent, the characteristics of the calcium cell and the excretory cell as described for some terrestrial pulmonates.

The narrow cell, described in other snails as an undifferentiated cell, resembles the flagellate cell of some prosobranchs. The presence of numerous parallel microtubules suggests a special function, e.g. structural, locomotory or sensory.

At the base of the gland epithelium cellular processes and occasional small cells are found that contain a number of small, (approximately 100nm diameter) electron dense granules. These could represent parts of endocrine cells or possibly aminergic nerve terminals; the latter suggestion being supported by the presence of microtubules in some of these processes.

Osmotic regulation and respiration in a marine pulmonate mollusc

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Amphibola crenata, a common air-breathing gastropod mollusc on mud flats exposed to wide variations in salinity, survives for many days in the laboratory in diluted and in concentrated seawater. In the range of 25% — 125% seawater, the osmotic concentration of the blood is ca 50 mOsm above that of the external medium and, in fresh water, is maintained at ca 280 mOsm. Equilibrium is achieved within ca 6 h of exposure to the

experimental medium. The volume of intracellular water, however, increases in diluted media ($\times 2.5$ in 25% seawater after 6 h) and decreases in hypertonic media. Complete cell volume regulation is accomplished after 6 h in 50% seawater, but is still incomplete after 9 days in 25% seawater. Intracellular volume is more easily adjusted in diluted media than in moderately hypertonic media (e.g. 125% seawater).

Oxygen consumption was related to body weight by the equation $VO^2 = aWb$. The slopes (b) of the log-log plots relating body size to oxygen consumption ranged from 0.43 — 0.46 and the 'proportionality factor' (a) ranged from 0.108 — 0.158 over the range 0-125% seawater. Oxygen consumption was not significantly affected by salinity. There is no significant difference between aerial and aquatic oxygen consumption. During exposure to declining oxygen tensions the snails were found to be oxygen independent, the degree of independence increasing with decreasing salinity. During exposure to anaerobic conditions the snails were found to build up an 'oxygen debt' which was subsequently 'repayed' upon return to aerated seawater. The oxygen debt reached a maximum after 6 hours hypoxia over the range 0-125% seawater. Small individuals with high metabolic rate are less independent of the ambient oxygen tension than larger individuals.

Uptake and Loss of Radium-226 in the Freshwater Mussel *Velesunio angasi*

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Velesunio angasi occurs abundantly in the aquatic environments in the vicinity of the uranium deposits in the Magela Creek system, Northern Territory. This mussel is a dietary component of the Aboriginal inhabitants. When mining begins it is expected that the levels of water-borne radium will increase. This study aims to obtain experimental data on the uptake and loss of radium — 226 in *Velesunio angasi*. Such data will allow the calculation of the level of radium — 226 in the mussel flesh for a known exposure time, radium concentration and certain other chemical parameters. Hence the potential dose to the Aboriginal consumers can be determined.

Aspects of the animal's biology that are likely to affect the levels of radium — 226 are also being investigated.

Samples of water, sediment and mussels have been collected for evaluation of base-line radium — 226 concentrations in a number of areas. Preliminary experiments have investigated.

- (i) the approximate rates of uptake and loss of radium — 226 by mussels
- (ii) losses of radium during the experiment (e.g. onto tank walls)
- (iii) variation in radium — 226 levels in water, food, mussel flesh and shell
- (iv) problems encountered in the use of mussels in laboratory experiments
- (v) loss of radium from mussels with high natural levels held in radium free water

Non-marine molluscs of S.E. Australia

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South-eastern Australia, consisting of Victoria, Tasmania and the parts of New South Wales and South Australia south of the 33°S parallel, constitutes a faunal region, the Peronian. Australia can be divided into six such regions, each with its own non-marine mollusc fauna. Each region is dominated by a different group of molluscs, showing a wide species radiation and a high proportion of endemism.

The non-marine mollusc fauna of South-eastern Australia consists of 39 families and about 210 species. The main families are the Hydrobiidae, Planorbidae, Rhytididae, Charopidae and Hyriidae. The Charopidae, with 54 species, is the dominant group for the Peronian region.

Examples of the variation and distribution within these groups are shown.

Factors influencing production of the cockle *Chione stutchburyi* in the Avon-Heathcote estuary, Christchurch, New Zealand

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The distribution (number m^{-2}) of the cockle *Chione stutchburyi* (Wood, 1828) in the Avon-Heathcote estuary, Christchurch, New Zealand (43°33'S, 172°44'E) is presented based on 200 quantitative sample sites. Relationships between total shell length, ash-free dry weight and age of 1000 individuals from a variety of growth conditions are discussed and are used to estimate the spatial distribution of *Chione* biomass (g ash-free dry wt m^{-2}) and production (g ash-free dry wt $m^{-2} yr^{-1}$).

The distribution of density, biomass and production are discussed in relation to the physical parameters of sediment composition (% mud, mean and median grain diameter of the sand fraction, and degree of sorting) and tidal position in an attempt to identify factors responsible for distribution and influencing production.

Consideration of each factor on two levels was found necessary. First, *Chione* tolerance limits to each factor were established on a "presence/absence" basis, thus defining the zone of intolerance. Second, using stations in which none of the factors are limiting, *Chione* preference to each factor was established, within the zone of tolerance, or regulation, based upon a peak in number, biomass and production.

Chione distribution was found to be restricted to below EHWN and to sediments with less than 50% mud and a mean particle diameter of the sand fraction smaller than 2.25 ϕ .

Sex in *Potamopyrgus*

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1. Introduction: It is accepted that in bisexual populations natural selection will keep the sex ratio to 1:1. Where parthenogenesis occurs alongside sex, the situation will be very different and it could be expected that the sex-ratio established would reflect the balance of advantage between sexual and non-sexual reproduction.

This poster presents for discussion observations on sex-ratios in natural and laboratory bred populations of the parthenogenetic hydrobiid *Potamopyrgus* from Europe, Australia and New Zealand, but interpretation is still not clear.

2. Natural Populations: A comparative table was presented of the percentage of males in populations sampled in the three areas. An Air photograph shows a small watershed in New Zealand that has been sampled for 9 years and gives yearly averages for males in neighbouring streams. This illustrates both the wide differences found even in similar habitats and the persistence of these from year to year.

3. Laboratory breeding: Females from the three areas have been kept alone or with males from their own or other regions. Sex-ratios found in the young bred have not always been the same as in the parent population(s). Figures are presented which suggest the following very tentative conclusions and interpretations:

A. Females held alone: generally produce daughters by parthenogenesis. Very few males have appeared but some at least may have been the result of prolonged sperm storage and/or embryonic diapause. One New Zealand locality has females showing little parthenogenesis.

B. Females held with males: generally also produce daughters, and present evidence suggests that these too are perthenogenetic, most captive males losing their fertility. Exceptions are the one N.Z. locality mentioned above, young from mated groups including many males. In another case where inherited colour gives evidence of paternity the young are largely male.

The significance of these findings for natural situations is not clear.